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Hilltopping by the Red Admiral Butterfly: Mate Searching Alongside Congeners

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Abstract. Males of the red admiral butterfly *Vanessa atalanta* (Nymphalidae) establish and defend territories in the late afternoon on a central Arizona hilltop. Resident males engage conspecific rivals in lengthy chases but respond less aggressively toward males of 3 congeneric species. A comparison between *V. atalanta* and 2 congeners, *V. annabella* and *V. cardui*, shows that the degree of site tenacity is correlated with the density of rivals. Males of *V. annabella*, the least abundant species, are most site tenacious, as measured by mean duration of residency and frequency of return to the peak. In contrast, males of *V. cardui* experience the highest hilltop densities and are the most ephemeral. Males of *V. atalanta* occur in intermediate density and exhibit intermediate site tenacity. Although male *V. atalanta* readily respond to any flying insect, the duration and complexity of these interactions is reduced. The various species also express different perch site preferences, which may aid in reducing the frequency of non-productive congeneric encounters.

Introduction

Hilltops serve as mate-encounter sites for a striking array of insects (Alcock, 1987; Shields, 1967). In many cases, including the red admiral butterfly (*Vanessa atalanta*), males perch along ridges and atop peaks where there is no concentration of resources useful to females (Alcock, 1984, 1987; Dimock, 1978; Shields 1967). Possibly hilltops act as orientation guides or dispersal barriers for species in which receptive females are otherwise evenly or diffusely distributed in the environment. In some regions, however, hilltops are unavailable and so male *Vanessa* butterflies adjust their mate-searching tactics by using alternative landmarks as territory centers (Alcock & Gwynne, 1988; Bitzer & Shaw, 1979; Palm, 1980). Where hilltops are absent, both *V. atalanta* and an Australian congener, *V. kershawi*, use landscape features such as sidewalks and forest clearings as points at which to search for mates. Thus, regardless of the local terrain, *Vanessa* butterflies appear to establish territories at places that are topographically distinctive.

Although different species of *Vanessa* have been reported to co-occur at hilltops (Dimock 1978; Shields 1967), little is known of the influence congeners may have on their mating systems. Here we report that *V. atalanta* interacts with other species of *Vanessa* (*annabella, cardui* and *virginiensis*) at a central Arizona hilltop. We describe the hilltopping behavior of male *V. atalanta* at this site with special attention to the

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Fig. 1. A view of the peaktop study site.

influence of congeners on mating system dynamics and examine if congeneric males have evolved ways to reduce potentially costly interactions with each other. We also compare the behavior of *V. atalanta* with *V. annabella* and *V. cardui*, and show a correlation between male density at the hilltop and the degree of site tenacity.

Methods

The hilltopping behavior of the *V. atalanta*, *V. annabella* and *V. cardui,* was observed on 69 days between 8 October 1988 and 13 April 1989. The study site was a dominant peak along Pima Ridge of South Mountain Park, Phoenix, Maricopa Co., Arizona (Fig. 1). Here the sparse vegetation was dominated by creosote bush (*Larrea divaricata*), brittlebush (*Encelia farinosa*), and staghorn cholla (*Opuntia acanthocarpa*).

At least one day each week, an attempt was made to record the arrival time of the first *Vanessa* of the day and the departure time of the last *Vanessa*, beginning the week of 20 October 1988. In addition, we analyzed interactions among the butterflies using the following procedure. Resident *V. atalanta* males were captured, given a unique mark on the upper side of the wing with colored liquid paper, and released within 2 min. They generally appeared undamaged by this treatment and either returned immediately to perch on the hilltop or flew off the peak. Once a marked *V. atalanta* male re-established residency, we recorded the durations of a single intraspecific interaction and a single congeneric interaction for 23 individuals. Starting from when the rivals were within ca. 10 cm of each other, we used a stopwatch to measure either the time one veered off the chase (i.e. a "drop", see Results, or a difference of greater than ca. 90° in their flight paths) or the time until the pair was lost from sight.

November and December 1988 were devoted to a comparative study of the site tenacity of *V. atalanta*, *V. cardui*, and *V. annabella*. Butterflies of each species were captured and marked. Sizes of individuals were categorized as either small, medium or large. Capture frequency gave a rough estimate of the relative abundance of each species on the hilltop. We also estimated the maximum number of each species of *Vanessa* at the hilltop at any one time during the afternoon. All previously marked butterflies that returned to the hilltop, both

those marked earlier that day and those marked on previous days, were recorded along with their time of arrival and duration of stay.

To analyze perch preferences of the 3 species, three 7 x 7 m quadrats were laid out on the hilltop, along the natural axis of the ridgeline (roughly east-west). The quadrats were immediately adjacent to each other and varied in altitude. Quadrat 1 (farthest east) was the peaktop; quadrat 2 was intermediate in altitude and quadrat 3 (farthest west) was at the lowest elevation, ca. 5 m below the peaktop. From 17 November to 13 February, we recorded the quadrats in which marked males perched after periods of flight. In addition to records of perch sites, the quadrat of capture was noted for each marked individual.

Means are reported ± 1 SE.

Results

SEASONAL TRENDS IN ARRIVAL AND DEPARTURE FROM THE HILLTOP

Both the arrival and departure of the first and last *Vanessa* on a given day are correlated with the time of year (Fig. 2). The butterflies arrived earlier as days shortened and later as days lengthed. This seasonal effect explains over 91% of the variance in hilltop departure times, the butterflies usually leaving within a few minutes of sunset. Arrival times, however, were not so predictable with only 50% of variance being explained by season, perhaps because of climatic effects. On relatively cool, windy days, arrival was delayed or the butterflies did not appear at all. On 12 days *V. atalanta* was absent on days of strong wind and heavy overcast, but returned on clear days later in the week. Shields (1967) also found a correlation between temperature, relative humidity, and the arrival time of *Vanessa* species.

Season also influenced the density of butterflies on the hilltop, measured both by the number captured and the maximum number observed at one time (Fig. 3). The density of hilltopping butterflies decreased as winter approached and increased again in the spring. The number of butterflies captured on a given day might have been influenced by both the density of butterflies and the duration of activity. However, because as days lengthened, butterflies postponed establishing residence on the hilltop until later in the afternoon, there was no relationship between date and duration of hilltopping activity ($r = 0.14$, $df = 11$, $p > 0.05$; mean duration of activity = 2.4 ± 0.2 h).

MALE-MALE ENCOUNTERS

V. atalanta males typically perched on the ground, on either stones or the bare ground. On especially hot days, males perched on hilltop shrubs. Resident males flew toward a variety of flying insects such as the wasp *Hemipepsis ustulata* and the hairstreak *Strymon melinus*, returning quickly to the perch if it was not a fellow *Vanessa*. Congeners, however, often elicited a chase, usually a quick, erratic flight across the peaktop. Chases were typically terminated when one individual veered away from its rival and returned to its perch. Resident *V. atalanta* chased heterospecific males for a mean period of 5.3 ± 1.1 s (N = 23).

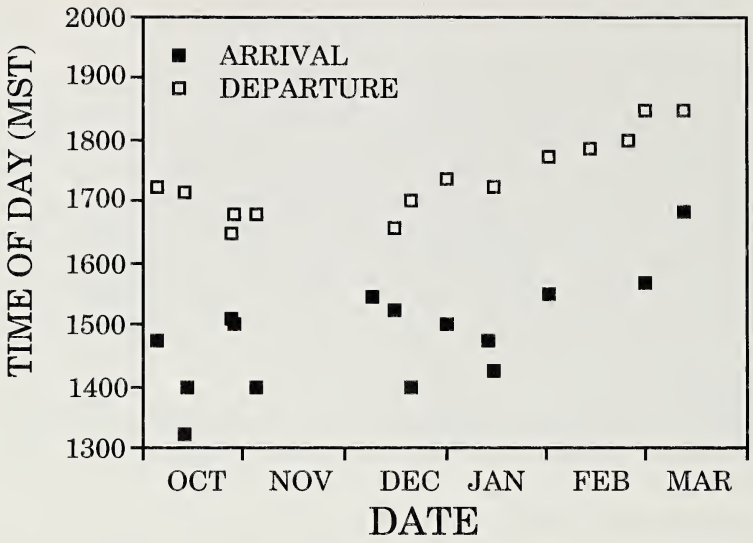

Fig. 2. The arrival time of the first *Vanessa* of an afternoon and the departure time of the last *Vanessa* of an afternoon, October 1988 to March 1989. For arrival, $r = 0.71$, $N = 14$, $p = 0.015$; for departure, $r = 0.96$, $N = 14$, $p < 0.0001$. Arrival and departure times were not species specific; results are consistent for each species ($p < 0.001$).

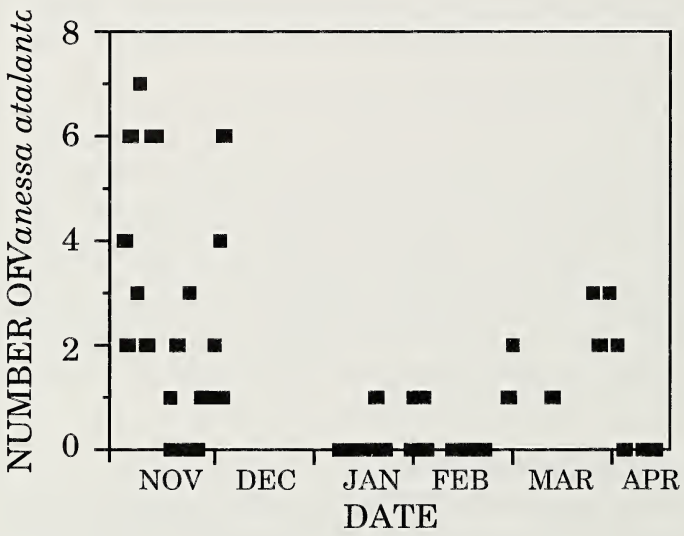

Fig. 3. Number of *V. atalanta* captured per day, November 1988 to April 1989; $r = 0.61$, $N = 53$, $p < 0.0001$. Regression of date versus maximum number of *V. atalanta* at any one time of an afternoon yields a similar result ($p < 0.0001$). Results are also consistent for *V. annabella* and *V. cardui* ($p < 0.05$).

In contrast, interactions between two *V. atalanta* males were often lengthy and complex. *V. atalanta* males chased conspecific rivals for a mean of 16.4 ± 3.7 s (N = 23), a significantly longer time than for heterospecifics (paired $t = 2.75$, $df = 22$, $p = 0.01$). After the initial approach, rival males often hovered for 1 or 2 s, one directly above the other, wings occasionally hitting, before entering into a prolonged chase. Chases took a variety of forms, from circles of the hilltop to sinuous chases along the ridge-line to long, ascending chases far off the peaktop. Conspecific chases ended when one of the pair dropped out of the chase, falling from the sky in a J-shaped dive, and either returned to the hilltop or continued on its way. Hovering occurred in 9 of 19 intraspecific and 0 of 19 congeneric interactions ($\chi^2 = 11.79$, $df = 1$, $p < 0.001$). Dropping out occurred in 13 of 19 intraspecific and 0 of 19 congeneric interactions ($\chi^2 = 19.76$, $df = 1$, $p < 0.001$).

MALE-FEMALE ENCOUNTERS

Male-female interactions differed markedly from interactions involving two males. Seven encounters between conspecific males and presumptive females were observed during the study (4 involving *V. cardui*, 2 with *V. atalanta*, and 1 with *V. annabella*). All male-female encounters were characterized by a slow, fluttering flight with the male following closely behind the larger female in a pattern highly reminiscent of *Chlosyne californica*, another hilltopping nymphalid (Alcock, 1985). These encounters began at the hilltop but all pairs subsequently flew downslope and were eventually lost from view. Unlike male-male encounters, the males failed to return promptly.

The courtships occurred as early as 1433 MST on 4 December and as late as 1650 MST on 10 April (Table 1). Moreover, a mating pair of *V. cardui* was sighted several hundred feet below the hilltop at 1803 MST on 29 March. Thus, courtship evidently does occur at the hilltop with female arrivals occurring throughout the period of male activity at the peak (see also Palm, 1980). Matings presumably occur downslope.

SITE TENACITY AND MALE DENSITY

A total of 114 *V. atalanta*, 215 *V. cardui* and 68 *V. annabella* were captured, with the numbers reflecting the relative densities of the three species. The degree of hilltop site tenacity was negatively associated with density of conspecific males at the hilltop (Table 2). The lower density species (*V. atalanta* and *V. annabella*)

Table 1. Times of *Vanessa* courtship

Species	Date		Time
V. annabella	4	December	1547
V. atalanta	28	November	1647
V. atalanta	4	December	1433
V. cardui	4	November	1645
V. cardui	16	January	1605
V. cardui	11	February	1622
V. cardui	10	April	1650

Table 2. Frequency of return to the hilltop and duration of stay for males of 3 *Vanessa* species.

Species	Day of Marking[1]	Male Returns On Subsequent Days[2]	Duration of Stay (min)[3]
V. atalanta	46 of 114 (40%)	24 of 114 (21%)	26.87 ± 4.73 (N = 46)
V. cardui	42 of 215 (20%)	14 of 215 (7%)	15.00 ± 3.24 (N = 42)
V. annabella	20 of 68 (29%)	15 of 68 (22%)	41.61 ± 6.49 (N = 20)

[1] $\chi^2 = 16.5$, df = 2, p = 0.0003
[2] $\chi^2 = 19.0$, df = 2, p = 0.0001
[3] ANOVA, F = 4.23, p = 0.007

tended to return to the hilltop after marking to a greater degree than the high density *V. cardui*. The pattern holds even when we exclude males that were marked within an hour of sunset: 24 of 45 (53%) *V. atalanta*, 15 of 29 (52%) *V. annabella*, and only 20 of 68 (29%) *V. cardui* were sighted again on the afternoon they were marked ($\chi^2 = 7.93$, df = 2, p = 0.019).

Similarly, the likelihood of return to the hilltop on days after marking was particularly low for *V. cardui* (Table 2). Whereas about 21% of *V. atalanta* and about 22% of *V. annabella* were sighted on at least 1 day after being marked, only 7% *V. cardui* males were resighted, a statistically significant result.

If they returned after being marked, males of the different *Vanessa* spp. also differed in the duration of stay at the peaktop (Table 2). Male *V. atalanta* remained at the peak for up to 152 min on a given afternoon, with an average of 26.87 ± 4.73 min (N = 46). *V. annabella* had the longest average duration of stay (41.61 ± 6.49 min, N = 20, range = 1 - 91), and *V. cardui* individuals were the most ephemeral with a mean duration of 15.00 ± 3.24 min (N = 42, range = 1 - 92).

Although male *V. atalanta* were relatively site tenacious, overthrows in hilltop possession occurred. Of 49 males that re-established residency after marking, 27 (55%) were unable to hold the hilltop territory for the remainder of the afternoon. Similarly, 9 of 21 (43%) *V. cardui* residents lost their perch (however, far fewer cases of sole residency occurred for *V. cardui* males). Again, *V. annabella* males were the most site tenacious with only 4 of 23 (17%) being overthrown. Frequency of turnover differed significantly among species ($\chi^2 = 9.07$, df = 2, $p < 0.025$).

Male longevity was much greater than individual tenure at the hilltop site. Male *V. atalanta* and *V. annabella* were re-sighted up to 21 days (N = 2) after their initial marking (N = 8 sightings of *V. atalanta* more than 14 days after marking). Thus, the failure of territorial males to hold their perch site over a period of days is puzzling. Previous residents seemed

not to have much advantage in holding the site when they did return on subsequent days. Eleven of 24 (46%) *V. atalanta* males, 8 of 15 (53%) *V. annabella* males, and 7 of 14 (50%) *V. cardui* males that returned on a subsequent day remained less than 10 min and failed to establish territorial residency, perhaps because they were ousted by younger, more energetic rivals.

No relationship exists between body size and measures of site tenacity. For neither *V. atalanta* or *V. cardui* does the likelihood of return to the hilltop vary significantly with size class (χ^2-tests, NS; data on *V. annabella* are insufficient for a similar test). Similarly, there is no apparent relationship between body size and frequency of return after capture for either of these species; sample sizes, however, are low and further tests are needed on this point.

PERCH PREFERENCES

The 3 species of *Vanessa* spatially separated themselves on the hilltop (Table 3). Both *V. atalanta* and *V. annabella* preferentially perched in quadrat 2, just below the peaktop. The numerically far more abundant *V. cardui* preferred the peak (quadrat 1). None of the *Vanessas* showed a preference for quadrat 3, the low elevation site. Although *V. atalanta* and *V. annabella* shared residency at quadrat 2, they consistently perched at the opposite ends of this section, *V. atalanta* towards the west at slightly lower elevation and *V. annabella* along the border of quadrat 1.

Male *V. atalanta* captured while perching in quadrat 2 were more likely to be sighted again that afternoon than were conspecific males perched in other sections of the peaktop ($G_{adj} = 7.84$, df = 1, $p < 0.01$). Males occupying region 2 tended to be residents that chased off intruders. These intruders often perched briefly outside the favored area of this species before departing.

Table 3. Perch preferences and capture sites of *Vanessas* at the hilltop.

Species	Perch Preference[1]			Capture Site[2]		
Quadrat:	1	2	3	1	2	3
V. atalanta	1	15	0	9	18	2
V. cardui	25	7	4	89	18	5
V. annabella	1	7	0	7	24	0

[1]Quadrat 3 is omitted to fit assumptions required for a G-test;
$G_{adj} = 30.4$, df = 2, $p < 0.0001$
[2]Quadrat 3 is omitted to fit assumptions required for a χ^2-test;
$\chi^2 = 51$, df = 2, $p < 0.0001$

Discussion

TEMPORAL PATTERNS OF MATE SEARCHING

In all 3 species, the abundance of males at the peak varies with the season, with the highest densities occurring at times of moderate temperatures (mid-fall and late winter). Males of all 3 species also exhibit similar daily patterns of mate-locating activity, with individuals arriving within 3 h of sunset and departing at dusk. Although receptive females arrive infrequenty at hilltops, they do so during the period when males are active at these locations. Perhaps late-day matings work to the female's advantage because they allow the protracted copulations to occur in the evening when they will not interfere with important daytime activities (Forsberg & Wiklund, 1989). Alternatively, males may limit mating activity to the late afternoon in order to reduce the likelihood of immediate remating by the female with consequent sperm dilution (Svard & Wiklund, 1988).

TERRITORIALITY BY HILLTOPPING MALES

While at the peaktops, males of the various *Vanessa* species appear to be territorial, a point that is particularly clear in the case of *V. atalanta.* Interactions between conspecifics of *V. atalanta* are far more complex and long-lasting than are interactions between heterospecifics, a result that matches that of Bitzer & Shaw (1979).

Scott (1986) has championed the alternative hypothesis that males are merely inspecting passing butterflies in the attempt to locate potential mates. This hypothesis has been critiqued elsewhere (Rutowski, 1984). Here we note that the sex-identification hypothesis produces the predictions that (1) male-male chases of any sort will follow much the same pattern as male-female pursuits prior to courtship, (2) when two males perch in the same area and then becomed involved in a chase both are likely to return to the perching area together, and (3) when only one male returns from a male-male chase, it is as likely to be one male as the other. All three predictions fail. (1) Male-female chases are very different in form from male-male interactions, which sometimes involve elaborate ascending flights with hovering bouts. (2) On a high proportion of chases, only one male returns to the perching area, not both. (3) When only one male returns, it is far more likely to be the established resident male, rather than a newcomer.

SPECIES DIFFERENCES IN SITE TENACITY

The congeners differed in their duration of residency at the peaktop and their frequency of return. Interspecific variation in site tenacity and the degree of territoriality was related to differences in the density of conspecifics at the peak. *V. annabella* was the most tenacious of the three species and was at lowest density on the hilltop; the relative lack of site tenacity shown by individual *V. cardui*, in contrast, was associated with the high density of conspecifics at the peak. *V. atalanta* exhibited moderate site tenacity and intermediate densities. Differences in con-

specific density were presumably associated with differences in the frequency of rival encounters. Thus, the differences in site tenacity and degree of territoriality of *Vanessa* butterflies may be caused by differences in how often individuals must deal with conspecific challenges at the mate-encounter site.

INTERSPECIFIC CONFLICT

Because a diversity of hilltopping insects have converged on the same site preferences (Alcock, 1983, 1984, 1987; Shields 1967), there is great potential for interspecific encoutners at a peaktop. Perched *Vanessa* males fly after most objects that pass by and thus spend much time and (presumably) energy responding to heterospecific insects. A similar response to moving objects has also been reported for other territorial butterflies (e.g. Alcock & Gwynne, 1988; Alcock & O'Neill, 1986; Davies, 1978; Lederhouse, 1982; Scott, 1974). It seems likely that this behavior is maintained because it enhances the rate at which resident males identify potential mates and conspecific rivals (Bitzer & Shaw, 1979). Alternatively, Bitzer & Shaw (1979) suggest that response to heterospecifics may function to reduce the costs of interspecific interference at the hilltop by chasing interspecific competitors from similar territory sites.

Because 4 species of *Vanessa* (*annabella*, *atalanta*, *cardui*, *virginiensis*) share the same central Arizona hilltops, the energy cost of heterospecific aggression is potentially great. Have these butterflies evolved any means to reduce non-productive interaction with congeneric males? Our observations show that territorial males can quickly distinguish rival conspecifics from congeneric males and have curbed the expense of interspecific aggression. Interactions between congeneric males are much shorter and much less aggressive than chases between conspecific rivals. Males of *V. cardui*, the most abundant species, are most often responsible for initiation and continuation of a congeneric chase and hence appear to be the least species-discriminating. Because *V. cardui* are so numerous at the study site, they interact with congeners less frequently than do either *V. atalanta* or *V. annabella*. Therefore *V. cardui* may be under less intense selection to be species-discriminating than are the other species of *Vanessa*.

Species-specific perch sites may also have evolved to reduce congeneric interference on the mating system. Perch site preferences of the three species were segregated on the peak and were not associated with nectar sources or oviposition sites. Turner (1990) has recently reported a similar spatial partitioning of the hilltop among swallowtail butterflies. However, rather than sorting themselves out horizontally, as in *Vanessa*, the swallowtails patrolled species-specific zones above the surface of the hilltop. Spatial separation on hilltops probably reduce the frequency of interaction between congeneric males. Further work is needed to determine if distinctive spatial preferences persist in the absence of congeners.

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